Genetic Improvement of Tomato

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General Importance

The tomato is a universally known vegetable and is one of the most widely grown. Its popularity is due in large part to its versatility and the variety it lends to the human diet. With the exception of potato (often classified as starchy staple), tomato leads all other vegetables in total production volume (Table 1).

Nutritionally, tomato may not rank high in concentrations of essential nutrients, yet, because of its popularity and diverse uses, it is an important alleviant of nutritional deficiency. In the United States, for example, tomato ranks only 13th and 16th among the main vegetables and fruits as vitamins C and A sources, respectively. However, it outranks all others in terms of total contribution of vitamins and minerals to the diet mainly on account of the high consumption volume for tomatoes, both in fresh and processed forms. In its own right, tomatoes have become almost a dietary staple.

Table 1. World production (x 1000 tons) of selected vegetables (1980 & 1987)

Crop	1980	1987
Tomato	50, 153	61, 363
Potato	225, 718	285, 009
Cabbages	35, 139	38, 132
Green beans	2, 428	3, 042
Peppers	6, 888	8, 740
Onions	19, 410	25, 282

Source: FAO Production Yearbook. 1980 & 1987.

Rick (1978) states "it is hard to realize now, when tomato is highly popular not only as a food in its own right but also as an ingredient of soups, sauces (including the ubiquitous catsup) and drinks, that as recently as 1900 it was widely avoided in the belief that it was poisonous because of its known relation to the nightshades and other toxic members of the nightshade family". Indeed, the story of tomato's transformation from an exotic fruit to a popular dietary item and a major commodity of commerce the world over is one of the most fascinating events in the saga of crop domestication. Its popularity is phenomenal and total production continues to rise in all four continents (Table 2).

Table 2. Trends in tomato production in different regions of the world

Region	Area ('000 ha) 1987	% Change (vs 1980)	Production ('000 tons) 1987	% Change (vs 1980)
Asia	832	+18.5	15,382	+29.8
Europe	448	-5.7	16,147	+10.8
North/Central America	307	+0.6	11,341	+23.3
South America	143	+10.9	3,718	+26.2
Africa	478	+27.8	7,240	+41.4

History of Domestication and Cultivation

All the cultivated forms of the tomato belong to *Lycopersicon esculentum*. It is generally accepted that the cultivated tomato originated from the New World (the Americas) since all related species of tomato are native to the Andean region now encompassed by the parts of Bolivia, Chile, Colombia, Ecuador and Peru. From these native habitats, tomato was taken to Europe soon after the discovery of the New World, very likely in already a fairly advanced stage of domestication. Writings as early as 1544 such as that of Mattiolus in Venice described a golden-fruited plant which was almost surely *L. esculentum.* A red-fruited form was described in a later writing. Furthermore, woodcuts from the early herbals clearly showed that the first types of tomatoes cultivated in Europe bore large fruits, typical of the tomato we know today. In contrast, all related wild species bear small fruits.

Evidence from the diversity of cultivated types and culinary uses and from the abundance of native names for the tomato fruit all suggest that tomato was originally domesticated in Mexico (Jenkins 1984). Its most likely ancestor is the wild cherry tomato (*L. esculentum* var. *cerasiforme*) which is spontaneous throughout the tropical and subtropical America and has later spread throughout the tropics of the Old World. Selection over many generations presumably led to increased fruit size and higher ratio of fruit weight to seed content that are typical of the modern-day tomato. The name "tomato" comes from Nahuatl language of Mexico and variants of this name have followed the tomato in its spread throughout the world (Heiser 1969).

Biosystematics of the Genus *Lycopersicon*

The tomato is a member of the Solanaceae or the nightshade family, a collection of some 1500 tropical and subtropical species probably originating in Central and South America. It is an important family as a food source (e.g. tomato and potato) although many of its members are characterized by relatively high concentrations of glycoalkaloid such as solanine, nicotine, scopolamine, atropine, tomatine, etc. The predominant alkaloid in the tomato is tomatine, which is at its highest concentrations in the foliage and the green fruit and is degraded to inert compounds on ripening.

Within the family Solanaceae, the genus *Lycopersicon* is a relatively small collection of species that are normally subdivided into two groups, the *Eulycopersicon* and the *Eriopersicon*. Fruits of the *Eulycopersicon* are usually red or yellow in color when ripe. The cultivated tomato, *Lycopersicon esculentum*, belongs to this group. In contrast, fruits of the *Eriopersicon* remain green or purple green throughout their development. At present, nine species are recognized as distinct entities within the genus *Lycopersicon* (Table 3). The first generally accepted description of several species of tomato, including the common one, was made by Miller in 1768; hence, various texts refer to the Latin name of tomato as *L. esculentum* Mill. in honor of Miller.

Genetic Diversity

Research on the nature of genetic diversity of *L. esculentum* has facilitated the understanding of the evolution of the cultivated forms and their further genetic improvement. The general agreement from such studies is that the cultivated and wild forms of *L. esculentum* are remarkably homogeneous (disregarding recent hybridizations with accessions from the native region) outside their native region of western South America. In contrast, more variation is present in the native region both within and between accessions. Several factors have been postulated to account for these differences: interbreeding with wild species in the native region; greater activity of insect pollinators promoting more outcrossing; effects of artificial selection; longer period of existence in the native region allowing the accumulation of more variants; and, genetic drift in the long migration from South America through Central America and Mexico coupled with natural selection for limited number of successful genotypes.

All members of the genus *Lycopersicon* are annual or short-lived perennial herbaceous diploids with a somatic chromosome number of 24. The cultivated tomato is a perennial plant normally grown as an annual. The genus as a whole tolerates a wide range of climatic conditions. For instance, *L. pennellii* (formerly *Solanum pennellii)* survives in very dry, rolling hills of western Peru whereas *L. cheesmanii* has been observed to grow in salt-laden atmospheres, just a few meters above the high water mark of the northwestern shores of the Galapagos Islands (Rick 1977).

In general, the relatives of the cultivated tomato have proven to be invaluable sources of desirable genes for further genetic improvement (Rick 1967; Rick 1981; Rick 1986). Examples of useful characters derived from the wild relatives of the tomato are as follows: jointlessness and salt tolerance from *L. cheesemanii*; high soluble solids from *L. chmielewskii*; resistance to Botrytis mold, Septoria leafspot and insect pests from *L. hirsutum*; TMV and rootknot nematode resistance from *L. peruvianum*; resistance to curly top virus from *L. chilense*; resistance to Fusarium wilt, gray leafspot, Cladosporium leafmold and spotted wilt virus from *L. pimpinellifolium*; and resistance to anthracnose, Alternaria collar rot, and Verticillium wilt from *L. esculentum* var *cerasiforme*.

The utilization of the above traits in improving cultivated tomato has been made possible by the ease with which interspecific crosses within and between groups is made (Table 4). Hybridization within the Group *Eulycopersicon* (red-fruited forms) show few, if any, barriers to gene exchange. The group is also crossable with members of the Group *Eriopersicon* (green-fruited forms) but in some cases, only when the latter functions as the pollen parents. This condition is termed "unilateral incompatibility". Where such incompatibility exists, the interspecific F_1 hybrid will hybridize with the cultivated *L. esculentum* only as a pollen par

ent; in crosses to the wild species, the F_1 hybrid is cross-compatible only when it serves as the female parent.

Successful intergeneric crosses have also been made between the cultivated tomato and its closely related *Solanum* species (Rick 1960; Stoeva and Zagorska 1987; Wann and Johnson 1963). A relatively loose barrier to gene exchange between species in the genus *Lycopersicon* and the feasibility of certain intergeneric hybridization with related *Solanum* species thus exist, albeit in some cases successful interchange may require the use of special techniques, e.g. embryo culture, tissue culture, bridging species (for wider crosses) , etc.

Table 3. General features of sub-genera of *Lycopersicon*

Sub-genus **Eulycopersicon**	Sub-genus **Eriopersicon**
The fruits are glabrous (hairless) at maturity and when fully developed are attractive in both taste and color, normally red or sometimes yellow; the plants are usually grown in cultivation as annuals although they can survive as perennials in frost-free conditions.	The fruits are whitish green in color, hairy and often with purplish tinge; generally not very attractive in appearance and flavor; the plants behave as perennials, dying down in adverse conditions to leave a woody stem base from which new growth emerges with the return of more favorable growing conditions.
Two species are included in the above subgenus: *L. pimpinellifolium* - currant tomato; fruits are 1 to 1.5 cm in diameter; both self- and cross-pollinated forms are known. *L. esculentum* - cultivated type; generally large-fruited but of varying sizes and shapes; self-pollinated; the wild form is *L. esculentum* var *cerasiforme* (commonly called the cherry tomato) – fruits are 1.5 to 2.5cm in diameter; the cultivated tomato is believed to have originated from this form, either directly or through hybridization with other species.	Seven species fall under the subgenus Eriopersicon: *L. cheesmanii* – self-pollinated; found only in the Galapagos Islands; fruits 6-9 mm in diameter; hybridizes easily with cultivated tomato; likely an intermediate form. *L. peruvianum* – self-incompatible; includes *L. glandulosum* ; fruits are 1 to 2 cm in diameter with lavender stripes down the midlocular axis. *L. hirsutum* – both self-fertile and self-incompatible forms known; fruits 1.5 to 2.5 cm in diameter with purplish longitudinal stripes; forma *glabratum* is self-fertile while forma *typicum* is more hairy and self-sterile. *L. chilense* – self-incompatible; fruits 1-2 cm in diameter; leaves binnatifid, covered with short hairs; inflorescence has typical long peduncle. *L. chmielewski* – cross-pollinated; fruits 1-1.4 cm in diameter; yellow-green color with relatively large calyx at maturity. *L. parviflorum* – self-pollinated; fruits are 1-1.4 cm in diameter with two dark green or purplish radial lines. *L. pennellii* – self-incompatible; formerly *Solanum pennellii*, this is another green-fruited species which hybridizes easily though unilaterally with cultivated tomato.

Genetic drift and selection for a few successful genotypes characterized the movement of tomato from its center of origin to the area of domestication and utilization(Rick 1978) . This genetic flow featured a series of changes in the floral structure–from well-exposed stigmas which facilitated cross-pollination in the primitive forms of *L. esculentum* to genetic fixation of a much shortened style in the modern cultivars (Figure 2).

The shortened style of present-day cultivated varieties places the stigma well within the anther tube, virtually eliminating the chance of outcrossing. Tomato is thus naturally highly self-pollinated. Rates of natural cross-pollination in the temperate zones vary from as low as 0.5% to as high as 4% (Rick 1978). In its native habitat in Peru, much higher rates of outcrossing have been noted because of the presence and greater activity of local insect pollinators.

The manipulation of the tomato for breeding and genetic purposes is fairly easy because its flowers are generally of good size and seed yield per fruit is high. Depending upon variety and environment, seed yield as high as 200 seeds per pollination is possible. Even without the use of mechanisms facilitating hybridity[2], e.g. male sterility and self-incompatibility, large scale production of hybrid tomato seeds is feasible because of the ease with which hybridization can be effected.

The optimum stage for emasculation of tomato flowers is a day before anthesis. Flowers at this stage have fully receptive stigma; their anthers and corolla normally show a color gradation from light to dark yellow and the sepals have begun to spread out from the bud. Dark yellow floral parts indicate fully mature flowers. Even with cautious handling, fully opened flowers should not be chosen for controlled pollination because the chance of inadvertent selfing is high.

Under isolated conditions of the greenhouse, emasculated flowers need not be bagged to prevent accidental outcrossing. The efficiency and success rate of indoor crossing are higher than in outdoor crossing. With the latter, it may also be necessary to protect flowers with glassine bags to avoid chance crosses. Cool, dry and relatively calm weather is generally favorable for field hybridization (Tigchelaar 1986).

Major Milestones in Tomato Breeding

Tomato was domesticated in Mexico and much of the credit for this very important early work must go to the native Indians who cultivated, consumed and improved the crop prior to its introduction to and adoption as a food crop in Europe and later in North America. In the latter areas, considerable progress arising from intensive research efforts happened as the crop's popularity steadily grew. In the United States, efforts by tomato scientists paid off with steady and dramatic increases in yield of processing cultivars (Figure 3). In California alone, new technology of production and improved varieties have led to four-fold increases in productivity of processing tomatoes since 1940, without which, processed tomato products would undoubtedly be a commodity that only a select few could afford (Tigchelaar 1986).

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[2] These hybridity mechanisms are present in the genus *Lycopersicon* but they have never been fully exploited in hybrid production. Self-incompatibility is a feature of several wild relatives (see Table 1) . Genetic male sterility is preponderant in the genus; many genes conditioning male sterility have been reported and described (Rick, 1956).

Table 4. Intra and interspecific breeding barriers in *Lycopersicon* [1]

♀/♂	*esculentum*	*pimpinellifolium*	*hirsutum*	*chilense*	*peruvianum*
esculentum	+	+	+	EA	EA
pimpinellifolium	+	+	+	EA	EA
hirsutum	+,UI	+,UI	+,SI,UI	?	EA
chilense	UI	UI	?	SI	EA
peruvianum	UI	UI	UI	EA	SI

+, no serious barrier; SI, self-incompatibility; UI, unilateral incompatibility; EA, embryo abortion; ? no known research results.

Reproductive Structures and Mating System

The tomato bears perfect flowers, i.e. it has both functional male (anthers) and female (pistil) organs (Figure 1). Several flowers are borne in an inflorescence; the number of flowers in an inflorescence may range from a few of 3 or 4 to as high as 50 in some of the cherry tomato lines (AVRDC, unpublished data). A single plant may produce as many as 20 or more successive inflorescences during its lifetime, thereby facilitating crosses among widely divergent cultivars since flowering occurs over a long period.

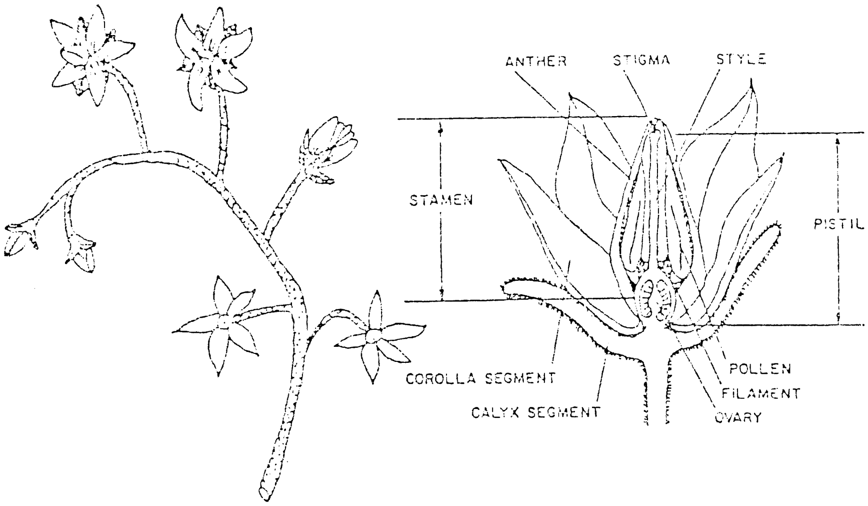

Figure 1. Diagrammatic sketch of a tomato inflorescence and flower showing all the essential parts.

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1 Adopted from Hogenboom (1972).

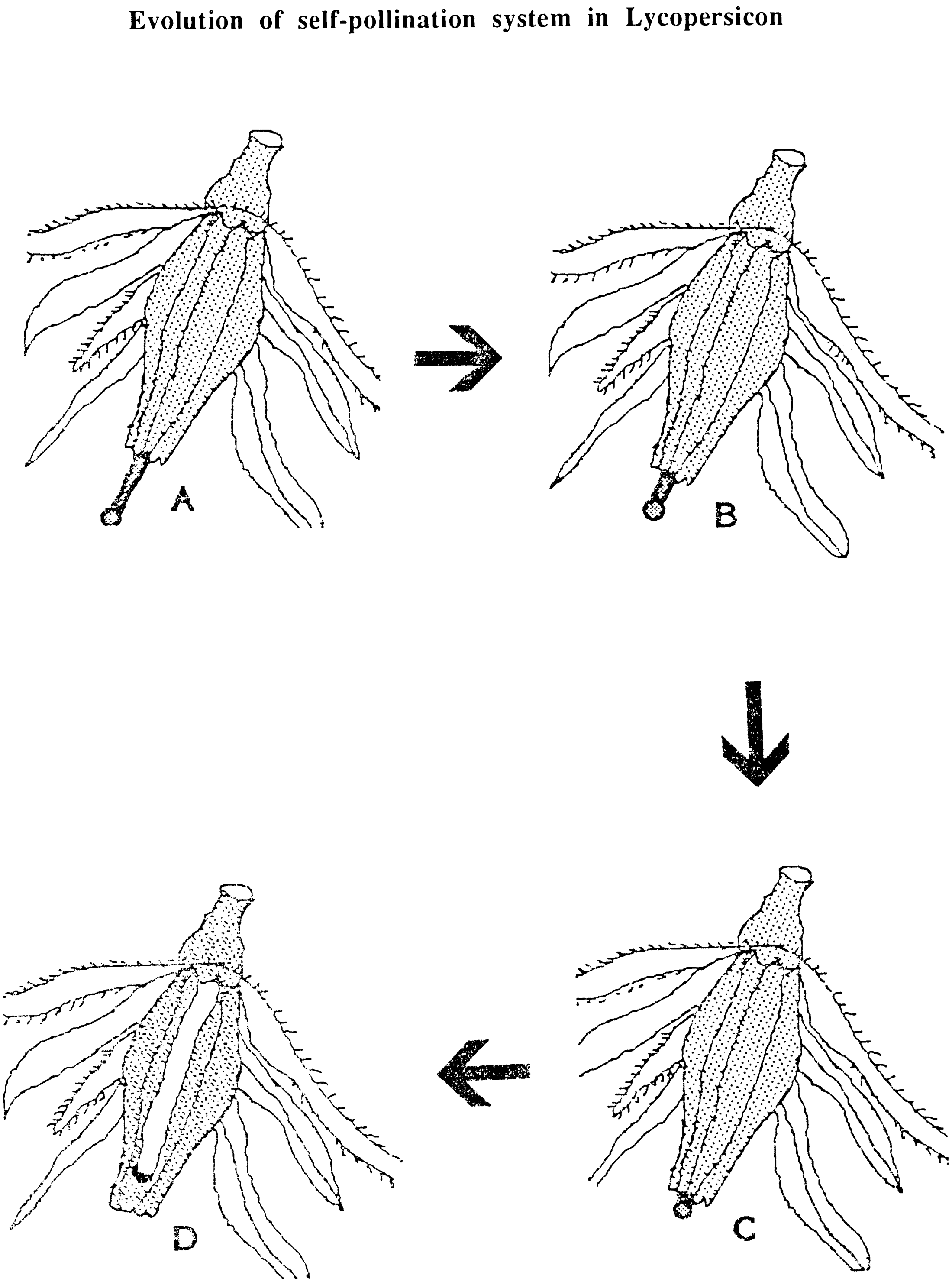

Figure 2. Progressive evolution of autogamous (self-pollination) mating system through the gradual shortening of the style, leading to well-inserted stigmas in the modern-day cultivars

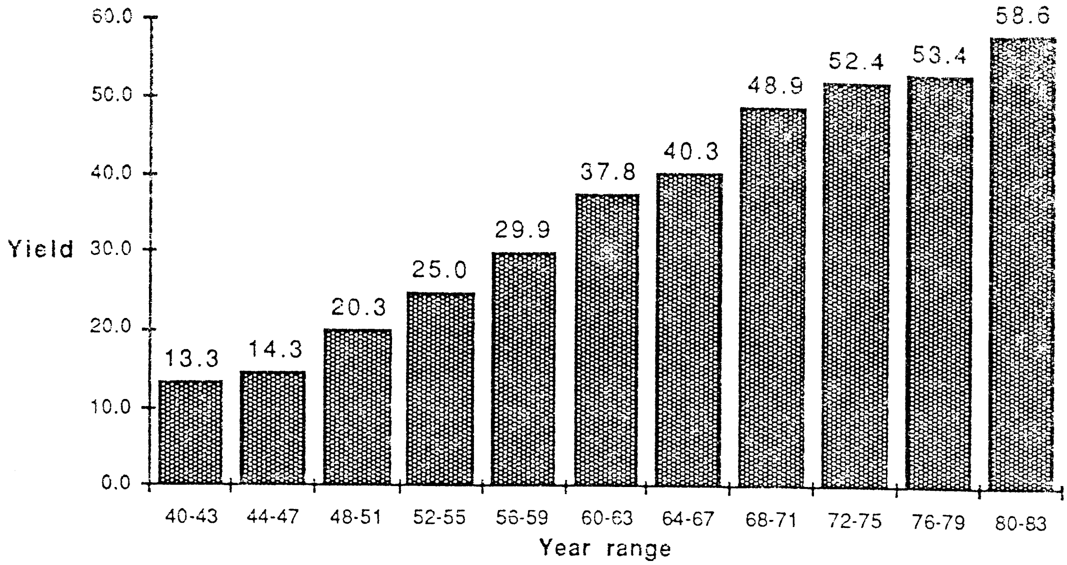

Figure 3. Progressive changes in the average yield (tons per hectare) of processing tomatoes in the United States (1940-1983)[3]

The substitution of a number of mutant genes in new cultivars has been a feature of the intense breeding activity since the 1940s (Rick 1978). One such example of a single gene with untold influence on the U.S. tomato processing industry is the self-pruning gene, *sp* , which causes the plant to grow in an orderly, compact, and determinate fashion. The *sp* gene appeared as a spontaneous mutation in Florida in 1914 and has been used in the development of a great number of cultivars in the last three decades. On account of its thrifty growth and more concentrated flowering, the determinate growth habit facilitates mechanical harvesting. Apart from changes in crop management and the design of a more suitable machine harvester, further breeding of determinate cultivars that have more compact growth, better concentration of set and with greater fruit firmness to withstand rough machine handling, along with the desirable yield, disease resistance and quality characters, paved the way for an efficient mechanization of the processing tomato production.

Other examples of major genes and polygenes that have contributed significantly in tomato improvement are given in Table 5. In particular, the genes for resistance to several major diseases have had great impact in the effective control of diseases for which chemical control has been ineffective or prohibitively costly. Good examples are resistance to soil-borne diseases such as bacterial wilt, Fusarium and Verticillium wilts.

The dominance of resistance genes for a number of diseases (among others, Verticillium and Fusarium wilts, rootknot nematode, Stemphyllium, Septoria, Alternaria, late blight, Cladosporium mold, and tomato mosaic virus) has also facilitated the development of F_1 hybrids with multiple disease resistance (Gilbert, McGuire and Tanaka 1961).

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3 Adopted and modified from Brandt (1978) and Sullivan (1977).

Table 5. Other examples of genes which have contributed to the improvement of tomato[4].

Gene designation	Gene symbol	Representative Cultivars / Lines
Dwarf	*d*	Tiny Tim
Jointless pedicel	*j-2* *j-1*	Many cultivars Penn Red
Septoria resistance	*Se*	Targinnie Red
Stemphyllium resistance	*Sm*	Chico III, Tecumseh
Leafmold resistance	*Cf* series	Many cultivars
Fusarium immunity Race 1 Race 2	 *I-1* *I-2*	 Pan American, Tainan No. 2 Walter
Bacterial wilt resistance	many recessive genes	Saturn, Venus, AVRDC tropical lines
Verticillium resistance	*Ve*	VR Moscow, VF series
Late blight resistance	*Ph-1*	New Yorker
Tomato mosaic virus resistance	*Tm-1, Tm-2, Tm-2a*	Many cultivars; AVRDC tropical lines (only *Tm-2a*)
Nematode resistance	*Mi*	Rossol, VFN Bush, many AVRDC tropical lines, many others
High pigment	*hp*	Redbush
High beta carotene	*B*	Caro-Rich
Non-ripening	nor^A	Long Keeper
Parthenocarpic fruits	*pat-2*	Severianin

In recent years, the use of F_1 hybrid cultivars has dramatically increased for fresh market tomatoes in Japan, Korea, Israel and in Eastern and Western Europe, and for processing tomatoes in California. As noted earlier, the ease of effecting crosses in tomato makes hybrid seed production feasible even with manual pollinations. As a matter of fact, virtually all hybrid seed production is manually done by highly skilled field workers. Some years ago, Taiwan was the world's leading producer of hybrid tomato seeds(Anon 1979). In recent years, however, rising cost of labor has made contractual hybrid seed production in the island comparatively expensive and contracting seed companies have begun to look elsewhere for alternative seed production sites.

While heterosis is generally minimal in self-pollinated species like tomato, the benefits of early ripening, improved vigor and the rapid development of improved cultivars which combine desirable traits such as disease resistance more than justify its exploitation in tomato improvement. Hybrid varieties also appear to have better consistency of performance especially under less than optimal growing conditions (Yordanov 1983). In addition, the added proprietary protection it gives to any new hybrid cultivar makes hybrid breeding a popular method among the private seed enterprises.

In recent years, the employment of biotechnological techniques has opened new vistas in tomato improvement that have never before been possible or would have taken long to

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4 Abridged and modified from Tigchelaar (1986).

achieve with conventional breeding. Examples of such advances are as follows: insertion of genes with insecticidal properties into the tomato genome; development of frost tolerant cultivars; and recently, development of tomatoes in which the gene that code for softening enzyme has virtually been deactivated causing the tomato to remain firm throughout full maturation. Continuing progress to 'tag' segments of the chromosome through techniques such as RFLP (restricted fragment length polymorphism) would also enable in the future an increasingly better control in manipulating complex traits and expediting the breeding process.

Commercial Types of Tomatoes as Breeding Targets

The versatility in usage and importance of tomatoes led to a great deal of specificity in developing appropriate cultivars for various purposes. Each of these purposes has, to a large extent, distinct requirements which demand fairly strict adherence before a cultivar could be successfully accepted by the growers. The distinctions between various commercial types of tomatoes are sufficiently clear that it is rare, if not outright impossible, to find a multi-purpose cultivar now. While certain objectives may still overlap, most tomato breeding programs are specially tailored to develop cultivars for specific purposes. The major types of tomatoes which serve as common breeding targets are discussed below.

Fresh market tomatoes. Tomatoes for fresh consumption have unique characteristics which depend a gerat deal upon the traditional consumer experience in the locality. In many western countries, fresh or table type tomatoes are preferably large, often more than 100 grams in weight, smooth, uniform shape, size and color, firm, good shelf-life for long distance shipping, and with good, tomato-like flavor. In some countries like Japan and Korea, pink-skinned tomatoes are preferred over the red tomatoes even though color has no known relationship to intrinsic quality.

It appears that the consumers' concept of tomato quality results partly from a general perception of the external appearance, with strong bias towards easily discernible features such as preferred skin color, rather than a definitive idea of intrinsic quality such as flavor and taste. In the United States, for example, the orange-fleshed cultivar Caro-Rich which has high vitamin A content was not accepted by the consumers even though masked color testing of the variety showed that it has comparable flavor as red-fleshed varieties (Tigchelaar and Tomes 1974; Tomes, Quackenbush and Kargl 1956). Despite the advantage in nutritional composition, it was not strong enough to override the bias towards red color. Studies in the United States indicate that flavor and taste of tomato is related to free sugars, organic acids and sugar-acid ratio (Kader *et al.* 1978; Stevens 1970; Stevens 1972; Stevens 1986; Stevens, Kader and Albright 1979; Stevens and Paulson 1976; Stevens and Rudich 1978).

In a number of tropical countries, sour, often small-fruited cultivars are preferred because they are used as ingredients in soups or local tomato-based sauces. In some cases, apparent preference for pink-colored cultivars such as in Thailand can also be noted.

Fresh market tomatoes often have indeterminate growth habit except in countries where mechanized or semi-mechanized field operations are practised. In the latter case, firm-fruited, semi-determinate cultivars such as Floradade or other later-bred cultivars are preferred as they are more amenable to mechanical operations. In some countries, determinate fresh market cultivars are grown even in the absence of an overriding need for mechanization because these are the only adapted cultivars available. Moreover, bush-type cultivars do not require costly and time-consuming staking and are thus preferred where farmers' capability to

provide inputs is limited. Where fruit quality is a premium, however, such as in large cities with substantial tourist industry to be served, indeterminate fresh market tomatoes are often demanded and cultivated.

Processing tomatoes. Tomato is processed into several major products (e.g. tomato paste, catsup, tomato juice, tomato sauce, etc) , each demanding special desirable features on cultivars that are grown for processing purposes.

In countries where the processing industry is very advanced, for example the United States or European countries like Italy, processing tomatoes are produced in extensive scale and highly mechanized, from production down to harvesting operations. Cost of manual labor in these countries are so high that mechanization appeared to be the only way they can be competitive in the international market.

To fit the cultivar to the mechanized operations, certain unique features need to be bred into them such as, among others, compact growth, firm fruits, concentrated fruit set and maturity, and ease of harvesting. These mechanization-related traits need to be combined with other desirable horticultural traits such as disease resistance, good canopy to minimize sun scorching, some level of stress tolerance to minimize split set and insure an undisrupted harvesting schedule, improved yield at no sacrifice in quality, earliness, etc.

Quality of processing tomatoes are normally measured in terms of color, soluble solids, pH, total acidity, total solids and viscosity. Some of these parameters are especially important for certain processed products. For example, viscosity (or consistency) is a primary quality attribute influencing catsup production. On the other hand, the tomato paste processing standard depends upon the final soluble solids content of the finished product, thereby demanding the use of high soluble-solids cultivars or adoption of management practices that maximize soluble solids of harvested tomatoes.

For less advanced processing tomato production, such as those in tropical and subtropical countries, the above-mentioned quality features are more often wished for but not necessarily obtained. Processing tomatoes under these conditions often have inferior color and relatively low solids content. Even with the use of cultivars of relatively high solids content, the growing conditions are not generally favorable for processing tomato production and management practices are not fine-tuned enough to achieve relatively high soluble solids content in the harvested tomatoes. Apart from processing quality, processed products are often insufficient for domestic consumption.,

Other special types. Tomato cultivars have also been developed for other special purposes, a glowing evidence of the popularity and the diverse business and personal interests of tomato growers and gardeners. For example, there are cultivars that are specifically bred for greenhouse production. These cultivars are generally indeterminate in habit and are productive for several months, medium to large-fruited, relatively uniform in size within the individual clusters, and carry resistance to diseases that are much more common in the greenhouse culture than in the outdoor production, such as tomato mosaic virus, leaf mold (*Fulvia fulvum*) , and gray mold (*Botrytis cinerea* Pers.).

Other diverse types that have been bred belong mainly to home-grown tomatoes and are developed to suit the fancy of consumers who prefer to savor the fruits of their toils by growing their own tomatoes in their backyard (home-garden type) or in small pots (patio-type tomatoes). Desirable features of these tomatoes include earliness, disease resistance, good quality, and prolonged production. In some cases, novelties such as unusual color (orange or yellow), dwarf habit for potted patio culture, unique fruit shape, etc. contribute to popularity of home-grown cultivars.

While cherry tomatoes are not new, recently bred cultivars have stimulated the interest of tomato growers in Japan, Korea, Taiwan and the United States. In Taiwan, cherry-type varieties, such as Girl Sweet and Len-tzu, are now grown by farmers for a special fresh use[5].

Common Breeding Objectives

High yield. Nearly every breeding program has high productivity as one of its major goals. Yield *per se* is the end product of a chain of interacting processes, each under a genetic system of control that may themselves be unique but often interrelated with the genetic systems underlying other processes. Genetically thus, yield is complex and invariably influenced by environmental factors.

The genetic control of yield is invariably polygenic (i.e. the trait is controlled by many genes with small effects and are highly influenced by environmental factors) ; also, additive and non-additively acting genes are known to condition yield. As a result, selection for high yield demands a rigorous control of environmental effects to insure that the phenotypic expressions of the breeding materials closely correspond to their true genetic potential.

Depending upon the predominant gene action, breeding techniques may be accordingly modified to attain maximum breeding gains. For example, where non-additive gene action is significant, hybrid breeding may be worthwhile to undertake especially if there are other overriding advantages of hybrid varieties in a given circumstance. On the other hand, conventional selection and development of standard open-pollinated cultivars prevail when additive gene action predominates, especially where seed companies do not play a major role in the vegetable seed industry.

Yield per unit area of tomato is a product of several components–plant stand, number of functional clusters, number of fruits per cluster, and fruit weight. Increasing yield may appear as simply maximizing each component. However, while each of these components may be linearly related to yield, they do interact with each other, often in compensating ways, resulting into a more complex rather than the simple arithmetic relationship between yield and its components. For example, increased fruit number per cluster or total fruits per plant means reduced mean fruit weight.

While yield components of tomato intimately determine gross yield, the final marketable yield is influenced by a number of other factors, mostly related to quality reduction. Defects such as sunscald, cracking, soft and diseased fruits, abnormal shapes, unattractive features such as fasciation and catfacing, poor color, and blotchy ripening contribute to the diminution of final yield. Therefore, breeding programs may effectively attain (or perhaps more appropriately, insure) high yield through obvious means such as breeding for resistance or tolerance to factors promoting these defects. Breeding for disease resistance also achieve the same effect–reducing disease-caused blemishes or rotting of fruits and maintaining the desired field stand.

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5 Cherry tomatoes are partly sliced and either date or bean sauce is placed inside to add to the flavor. Fruits, in general, are sweet and crispy (on account of thick and tough skin).

Tolerance to biotic stresses. Biotic stresses refer to all disease and pest factors affecting the productivity of tomatoes. No doubt, biotic stresses are among the major yield and quality-limiting constraints, if not the most important, in tomato production. In view of this, tomato breeding programs always include breeding for pest resistance, especially disease resistance, as one of the major objectives.

The development of disease-resistant tomato cultivars is perhaps one of the most important contribution of modern plant breeding to tomato improvement (Tigchelaar 1986). There are a number of economically important diseases for which control is either absent or prohibitively costly (e.g. soil-borne wilt diseases such as bacterial wilt, fusarium wilt, etc). Exploitation of host plant resistance in breeding gave rise to resistant cultivars which made production in infected fields economically feasible. With the vital collaboration of plant pathologists, tomato breeders have successfully bred increasingly more disease-resistant breeding lines.

Progress in developing disease-resistant tomatoes would not have been possible without the genetic resources to sustain the breeding efforts. Fortunately, the genus *Lycopersicon* is a treasure trove of genetic variability (see Section Genetic Diversity). Genes for resistance to various diseases have been uncovered from cultivated and wild relatives of tomato and in many cases, their underlying inheritance are also well known (Table 6; see also Table 5 for examples of genes controlling resistance to several diseases and resistant cultivars).

While much of the advances in tomato research, particularly disease resistance, has been achieved in the temperate countries, the tomato research at AVRDC in Taiwan has undoubtedly contributed to enable profitable tomato production in the tropics. A great part of this feat owes much on the early development of breeding lines that are resistant to bacterial wilt, followed by a progressive pyramiding of additional genes for resistance to other major tropical diseases, particularly tomato mosaic virus and common rootknot nematode (Opeña, Kuo and Yoon 1987a; Opeña *et al.* 1988; Opeña *et al.* 1987b). The incorporation of additional resistance to diseases such as bacterial spot (*Xanthomonas campestris* pv. *vesicatoria*), black leafmold (*Cercospora fuligena*) and potato virus Y is underway and stands to further improve the reliability of tomato production under adverse tropical growing conditions.

Insect resistance breeding in tomato has not been as successful as disease resistance breeding. The difficulty does not appear to be due to restricted variability for insect resistance; as a matter of fact, the genus *Lycopersicon* is replete with good reports on resistance to various mites and insect pests (Table 7). Several reasons attribute for the lack of progress in insect resistance breeding: first of all, insect resistance has traditionally received low priority in applied breeding programs because the use of pesticides has effectively controlled most of the major insect pests of tomato; in addition, the screening and selection methods to exploit the existing genetic variability for insect resistance are difficult to develop.

With the exception of a few cases, the genetic resources for insect resistance in tomato exist mainly among the wild species (see Table 7). Of these wild relatives, the most prodigious reservoir are the species *hirsutum* and *pennellii*. Efforts to utilize these species to breed insect-resistant tomato breeding lines are now underway at AVRDC for pests such as fruitworm (*Heliothis zea*) and aphid (*Myzus persicae*) . The potential impact of insect-resistant

Table 6. Sources of resistance and inoculation techniques for screening tomato diseases[6]

Disease	Causal organism	Source of resistance	Inoculation techniques
Fusarium wilt	*Frsarium oxysporum f. sp. lycopersici* (Sacc.)	Pan American (race 1), Walter (race 2)	Dip roots in inoculum and transplant to flats
Verticillium wilt	*Verticillium albo-atrum* Reinke & Berth	VR Moscow	Dip roots in inoculum and transplant to flats
Late blight	*Phytophthora infestans* (Mont.) DBy	West Virginia 63	Inoculate leaves with swarmspore suspension by atomization
Early blight	*Alternaria solani* (Ell. & G. Martin) Sor.	(on foliage) 68B134	Inoculate with atomized spore suspension
		(collar rot) Southland	Dunk tops and stems of seedlings into inoculum and transplant to a depth of 3 in
Septoria leaf spot	*Septoria lycopersici* Speg.	Targinnie Red	Atomize conidial suspension onto plants
Gray leaf spot	*Stemphylium solani* Weber	Manalucie	Atomize spore suspension onto plants
Leaf mold	*Fulvia fulvum* Cke.	Sterling Castle	Inoculate by spraying lower-leaf surfaces with spore suspension
Foot and stem rot	*Didymella lycopersici* Kleb.	*L. hirsutum* 66087 (IVT 61292)	Apply 3 ml of inoculum around the stem base of 1-week-old seedlings
Brown root rot (corky root)	*Pyrenochaeta lycopersici*	PI 260397	Plant to fields infested with the causal organism
Anthracnose	[*Colletotrichum phomoides* (Sacc.) Chester] C. *coccodes* (Wallr.) Hughes	PI 272636	Inoculate fruit by atomization or puncture
Rhizoctonia soil rot	*Rhizoctonia solani*	PI 193407	Place mature green fruit on infested soil

(Continued)

6 Adopted from Webb *et al.* 1973.

Disease	Causal organism	Source of resistance	Inoculation techniques
Bacterial wilt	*Pseudomonas solanacearum* (E.F. Sm.) E.F. Sm.	PI 127805A Saturn Venus	Cut roots on one side; pour bacterial suspension into soil trench
Bacterial canker	*Corynebacterium michiganense* (E.F.Sm.) H.L.Jens.	Bulgarian 12, Utah 737	Inoculate cut made by excising first true leaf at point of attachment with bacterial suspension
Bacterial speck	*Pseudomonas tomato*	Ontario 7710	Atomize suspension of *P. tomato* on both sides of leaf
Tomato mosaic	Tobacco mosaic virus	Ohio M-R9	Apply expressed inoculum with an air brush; inoculate again 10 days later
Spotted wilt	Spotted wilt virus	Pearl Harbor	Place seedlings in a disease nursery and encourage thrips
Curly top	Curly top virus	CVF 4	Release viruliferous leafhoppers into screened green house 2 or 3 times at 1-week intervals
Yellow leaf curl	Yellow leaf curl virus	*L. pimpinellifolium* (LÁ 121)	Release viruliferous whitefly females onto caged tomato seedlings; allow feeding for 72 hr.

cultivars in the tropics is tremendous, considering the relative difficulty and prohibitive costs of controlling pests by inorganic chemicals. Eliminating the use of pesticides that are generally hazardous to health and threatening to the integrity of our environment is probably the most noble justification to intensify the efforts in insect-resistance breeding.

Apart from diseases and insects, tomato is also attacked by nematodes, causing devastating losses where they are endemic. Among 37 recognized rootknot nematode species (*Meloidogyne* spp), seven are known to attack tomato of which *Meloidogyne incognita* is the most prevalent and of major importance in tomato production (Taylor and Sasser 1978). Losses due to direct infection (Bailey 1941; Baker, Shoemaker and Nelson 1976; MacFarlane, Hartzler and Frazier 1946) and indirect losses due to predisposition or breakdown of resistance to other root diseases, e.g., bacterial wilt (Gilbert, Tanaka and Takeda 1974) are significant. Much like many other diseases, breeding for resistance offers the most economical long-term solution.

Table 7. Genetic resources for resistance to various mites and insect pests of tomato.[7]

Insect pest	Source of resistance	Species
Flea beetle (*Epitrix hirtipennis*)	PI 126449	*L. hirsutum* f. *glabratum*
Potato aphid (*Macrosiphum euphorbiae*)	PI 129145	*L. peruvianum*
Spider mite (*Tetranychus telarius* L.)	Anahu	*L. esculentum*
Carmine spider mite (*Tetranychus cinnabarinus*)	Several accessions	*L. hirsutum*
Colorado potato beetle (*Leptinotarsa decimlineata)*	PI 134417	*L. hirsutum*
Pinworm (*Keiferia lycopersicella)*	PI 127826	*L. hirsutum*
Leaf miner (*Liriomyza munda)*	PI 126445, PI 126449	*L. hirsutum* f. *glabratum*
Fruitworm (*Heliothis zea)*	PI 126449	*L. hirsutum* f. *glabratum*
Tobacco hornworm (*Manduca sexta* L.)	PI 134417	*L. hirsutum* f. *glabratum*
Whitefly (*Trialeurodes vaporariorum*)	IVT 74453 IVT 72100	*L. hirsutum* *L. pennellii*

Bailey (1941) reported *L. peruvianum* as a source of resistance to rootknot nematode. The first interspecific hybrid between *L. peruvianum* and cultivated tomato was made in 1944 using the former as male parent to overcome the unilateral incompatibility barrier and rescuing the immature embryo through aseptic culture to surmount hybrid breakdown (Smith 1944). Further backcrosses using cultivated tomato as the male parent led to the independent development of cultivars VFN-8 and Anahu in California and Hawaii, respectively. This resistance is controlled by a single dominant gene *Mi* (Barham and Winstead 1957; Gilbert and McGuire 1956) and provides resistance to three other prevalent nematode species (*M. javanica, M. arenaria,* and *M. acrita*).

A tight linkage between the *Mi* gene and *Aps-1*, a variant locus of acid phosphatase isozyme was discovered on cv. VFN and other nematode-resistant cultivars (Rick and Fobes 1974). This discovery led to the practical use of electrophoresis in screening for nematode resistance in the laboratory to complement or replace other methods of resistance screening that had been proposed in the past (Bailey 1941; Dropkin, Davis and Webb 1967; Fassuliotis and E. C. Corley 1967). A number of resistant cultivars from many sources were studied (Medina-Filho and Stevens 1980) ; cultivars with pedigrees tracing back to Hawaiian materials did not show the *Aps-1* band pattern. On the other hand, those derived from California resistant stocks maintained the linkage relation between *Aps-1* and *Mi* genes. A linkage test between these genes was carried out and it was concluded that nematode resistance screening

[7] Modified after Tigchelaar, 1986.

based on the *Aps-1* banding pattern was remarkably reliable (Medina-Filho and Stevens 1980).

Tolerance to abiotic stresses. Tomatoes thrive and produce well under generally cool and dry climate. Any significant deviations from this ideal condition, sush as high temperatures and excessive rainfall, generally result into depressed tomato yield and quality. Fruit set is one of the key components of final yield in tomato (Picken 1984; Stevens and Rudich 1978) that is greatly affected by adverse conditions, particularly high temperature (Opeña *et al.* 1987a). Both night and day temperatures are considered important to tomato fruit set (Sugiyama, Iwahori and Takahasi 1966). Maximum temperatures below 30°C favored fruit setting and yield; ranges between 30°-45°C markedly reduced fruit set (Went 1945). Poor fruit set at high temperature might result from the reduction of carbon export from the leaf and the inability of reproductive organs to import assimilates in the early stages of flower development (Dinar and Rudich 1985; Dinar, Rudich and Zamski 1982).

Heavy rainfall may mechanically damage the aerial parts of plants, but topogenic water accumulation due to poor surface drainage may also lead to damaging flooded conditions. One principal effect of flooding is the rapid depletion of soil oxygen supply from the roots. The effect of oxygen deficiency on plants is complex, comprising of direct, physiological effects of low oxygen supply, and the indirect, oxygen-dependent changes in the soil; these factors are difficult to separate. Visual symptoms due to deficient aeration may appear on the roots and shoots. The characteristic symptoms of flooding damage in the tomato shoots are: a) reduced stem growth; b) chlorosis of the lower leaves; c) marked epinastic curvature or wilting of the leaves; d) production of adventitious roots; and e) death of the plants.

The primary cause of the above growth disturbances is the inhibition of aerobic respiration in the roots (Drew 1979). Other adverse effects on the plant's vital functions such as growth, water uptake, and nutrient uptake, are the consequences of abnormal respiration. The exclusion of oxygen from root metabolism also causes ethanol accumulation and ethylene elevation (Bradford and Yang 1981). Toxic effects of ethanol on plant tissues and the association of ethylene, epinasty, and adventitious root formation are known (Kuo and Chen 1980; Kuo *et al.* 1982).

Breeding for stress tolerance in tomatoes, particularly to high temperatures, has been carried out at AVRDC since 1972. Heat tolerance in tomato was defined as the ability to set fruits under night temperatures not lower than 21°C (Villareal and Lai 1978). This trait reportedly gave strong indications of genetical complexity–variation was continuous and heritability values were low, with a range of only 5–19% (Villareal and Lai 1978).

Defined on the basis of fruit set, heat tolerance implies an ultimate product of a complex reproductive process; therefore, attempts have been made in the past to examine the components, rather than the end product of the trait, so as to deduce relatively simple genetic situations. For example, stigma exsertion, one of the common responses of heat-sensitive cultivars under high temperatures, was found to be controlled by partially dominant genes with high additive component and heritability (El Ahmadi and Stevens 1979; Levy, Rabinowitch and Kedar 1978; Stevens 1979). These results corroborated well with the outcome of an earlier study (Rick and Dempsey 1969).

Further studies of a genetically diverse seven-parent diallel set showed that both additive and non-additive genes are important in regulating the fruit set at high temperature (AVRDC 1988). A similar genetic behavior was noted for the splitting of the antheridial cone, a common reaction of tomato flowers to high temperature.

Based from the above study, it was concluded that both conventional breeding methods, which take advantage of additively acting genes, and hybrid breeding, which relies primarily on genetic interactions, should be effective in breeding for heat tolerance. In support of the latter, about 1/3 of the diallel hybrid progenies from the foregoing study had better fruit set than the better heat tolerant parents (AVRDC 1988).

In a related study, crosses between heat tolerant stocks were noted to have better fruit setting ability and yield than their crosses with heat sensitive parents (Figure 4). However, it was apparent from the range of F_1 means (Table 8) that some hybrids between heat tolerant and heat sensitive stocks could equal, if not surpass, the performance of hybrids among heat tolerant stocks, further supporting the results from the diallel experiment (Opeña *et al.* 1987a).

Improved Quality. Aiming for improved quality through breeding is freqrently only a wishful thinking because the parameters that affect quality are generally nebulous. Moreover, the criteria of good quality vary among consumer groups. The subjectiveness of quality introduces a great deal of complications in its genetic improvement. Quality is, therefore, often only a secondary priority in the breeding program. Nonetheless, every breeder must insure that the resulting product of breeding must, at the very least, conform to the acceptable norms of quality. Often, this involves merely insuring that the new culitvars are not exceedingly off-flavored or of poor external appearance.

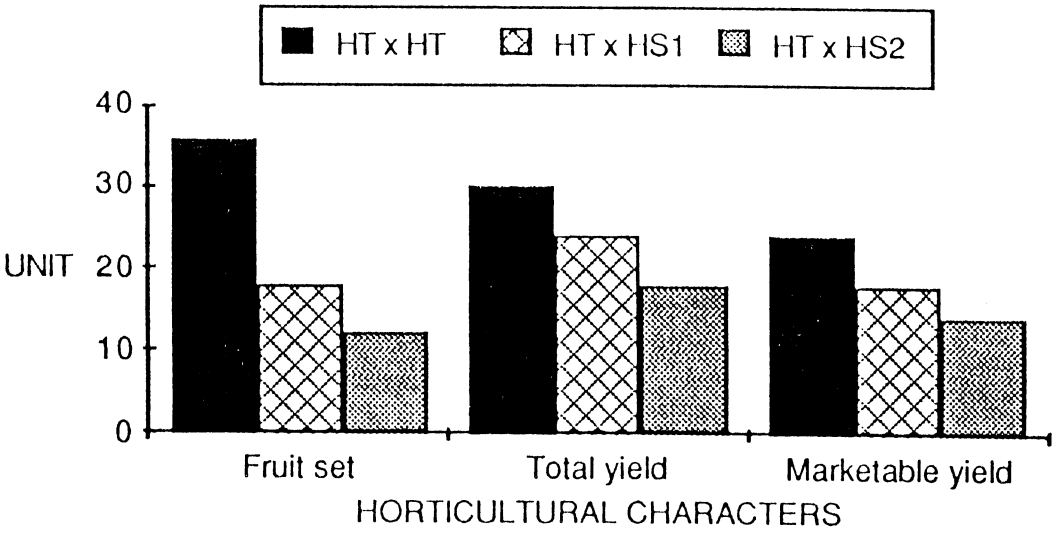

Figure 4. Comparative fruit set (%) and yield (t/ha) of F_1 hybrid progenies derived from crosses among parents with varying levels of heat tolerance (abbreviations in the legend footnoted in Table 8).

Table 8. Range of values for different characters among tomato hybrids with differing levels of heat tolerance (exceptional upper range values are underscored).

Type of cross[z]	No. of crosses	Fruit set (%)	Yield (tons / hectare) total	Yield (tons / hectare) marketable	Fruit size (g)
HT / HT	8	26-52	15.4-37.5	12.3-29.0	41-63
HT / HS1	11	5-30	15.9-28.8	9.8-23.2	57-83
HT / HS2	10	2-32	6.3-33.2	5.9-27.6	59-92

[z] HT = heat tolerant parent; HS1 = heat sensitive parent (less than 10% fruit set) ;
HS2 = heat sensitive parent (no fruit set).

While the above may be a common scenario in tomato breeding, there are aspects of tomato quality that could be reasonably improved in a breeding program. The tomato fruit is about 95 to 96% water. The remaining 4 to 5% are comprised of organic constituents such as organic acids, free sugars and volatiles. This fraction generally gives the tomato fruits its unique flavor, taste, aroma and texture (Stevens 1979; Stevens *et al.* 1979; Stevens and Rudich 1978). Dramatic changes occur on these constituents as the tomato fruits mature. There are indications that some, if not all, of these constituents are fairly simple in inheritance and are, therefore, amenable to genetic improvement (Stevens 1970; Stevens 1972; Stevens 1976; Stevens 1986).

Breeding for improved appearance often receives higher priority over the intrinsic aspects of quality. This is understandable when one considers that consumers often have bias towards what they can see and perceive. Size, shape, external color, smoothness of the fruit surface, firmness, uniformity and freedom from defects such as cracking, catface and fasciation are generally important breeding objectives especially for table tomatoes. Some of the above may also be important for processing tomatoes (such as fruit color, firmness and crack resistance) but generally less so than with fresh market types since tomato fruits for processing are crushed and concentrated into various processed forms.

Considerable progress has been obtained in developing cultivars that are both firm and resistant to cracking (Reynard 1960; Scott 1983). With respect to fruit color, many genes affect the trait (Darby 1978) , of which, for practical purposes, genes *hp* and og^c have been explored to enhance the redness of tomato fruits (Thompson 1961). With good practise, both *hp* and og^c may be visually assessed among breeding progenies. Gene og^c increases the red pigment "lycopene" but does so at the sacrifice of reduced β-carotene and thus, lower vitamin A content of the fruits. In contrast, gene *hp* increases total carotenoids thereby rendering excellent color to the fruit and enhanced vitamin A content. However, several undesirable pleoitropic effects of *hp*, such as slow germination, thrifty growth, and premature defoliation, have discouraged its use in tomato improvement programs (Kerr 1965; Sayama and Tigchelaar 1985; Wann *et al.* 1985).

Breeding Techniques

The most fashionable breeding technique to improve tomato has been hybridization followed by pedigree selection. Single-seed descent method was developed later and has been used as an alternative to pedigree selection where facilities or funds do not permit copious and time-consuming record-keeping from breeding materials, or to develop a diverse range of "ready-to-test" breeding lines for trial and selection by national programs which lack breeding expertise to undertake full-scale breeding programs (Villareal and Lai 1979) , or where facilities to maintain winter breeding nurseries are limited (Tigchelaar 1986). Backcross breeding has been the method of choice when desirable traits are to be transferred from the wild species or from relatively unimproved cultivated varieties. In some breeding programs, combinations of methods such as pedigree breeding and single-descent have been found to be a useful approach (Casali and Tigchelaar 1975). A number of breeding techniques are further discussed below.

In most cases, the breeder's goal is to develop improved standard, open-pollinated cultivars. However, in the last decade or so, the use of hybrid cultivars has increased dramatically that in several countries, they have almost replaced the standard cultivars in fresh market tomato production (see Section Major Milestones in Tomato Breeding). The major role played by the private seed sector in developing and distributing improved tomato cultivars has encouraged the trend towards increasing use of hybrids. Irrespective of the final type of cultivar to be developed, the breeding techniques that are used to develop the improved standard cultivars and/or inbred parents for hybrid varieties are one and the same. In developing hybrid varieties, however, this is further extended to select from among the inbred stocks those that nick well to produce superior hybrid progenies. This normally entails the application of progeny testing methods such as combining ability test, especially where a great number of parental stocks are being exploited. In certain situations, conscious breeding for traits which facilitate emasculation of tomato flowers, such as genic male sterility, may also be done as an accessory of hybrid breeding.

Selection methods for naturally occuring variation. Old land varieties or, even local cultivars that have been grown for sometime under a certain environment without conscious selection by farmers themselves, are considered as populations of pure lines[8]. Before any long range breeding program of hybridization and selection is conceived, plant breeders must first explore the genetic materials on hand. Old local cultivars which have well-proven adaptability under certain conditions are often available. Sometimes, introduced cultivars which do well under a particular condition may exhibit some degree of utilizable variation. Breeders need to examine these materials closely to see if simple selection procedures can bring in further improvement. When substantial variation is available, mass selection will allow the elimination of undesirable individuals and, at the same time, preserve the characteristics that have made these cultivars successful. Afterwards, pure line selection could be applied to further identify the most superior, homozygous lines for eventual release to the growers.

Mass selection. This may be achieved by simply growing the variety in the field and roguing out the undesirable types. At maturity, the remaining plants (presumably the good plants) are bulked. A modification is tagging only the best plants in the field and bulk-

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8 Technically, a pure line is the collective term for progenies of a single, self-fertilized homozygous individual.

harvesting them at maturity. The two methods are essentially similar, the only difference being in the level of selection intensity. Modern plant breeding usually employs mass selection to preserve the characteristics of established varieties.

Pure-line selection. This is a refinement of mass selection. The method involves also tagging (selecting) the best plants of the variety. However, instead of bulk-harvesting these plants as in mass selection method, they are harvested separately and evaluated as distinct progeny rows (pure lines). Only the superior pure line is bulked as an improvement of the variety. The pure line may even be released as a new variety if it is sufficiently different from the original variety.

Selection methods for variation generated through controlled hybridization. Following hybridization, a tremendous burst of variation is released after selfing the immediate hybrid progeny of the cross. Successive self-fertilizations of the hybrid progenies of self-pollinated crops lead to the progressive decay of the variability within individuals, but with concomitant accentuation of the variation among individuals. The variability can be managed by different methods, ranging from simple systems (such as single-seed descent and bulk method) to more tedious and elaborate techniques (such as the pedigree method). Each technique has its own merits and demerits and their application depends upon a number of factors such as manpower, land and financial resources, level of expertise, timetable, objectives, crop species, etc.

Pedigree method. As the name denotes, pedigree method involves taking a record of the line of descent (or "pedigree") of individuals or lines selected in each generation. These notes are very important in deciding which lines to keep or eliminate. The information to accumulate may range from notes of general vigor, maturity, resistance to some diseases or pests, quality, etc.

The pedigree method offers the plant breeder an opportunity to sample families of diverse descent. For example, if two lines behave similarly, one could be eliminated if they are closely related according to the pedigree record. This aid in decision-making offered by the pedigree record clears the way for the breeder to select another unrelated line out of the same cross.

In using pedigree selection, the breeder must keep in mind the changing architecture of variability. The greatest range of variability will be expressed in the F_2 generation; thereafter, the level of heterozygosity in the population will decrease rapidly upon selfing with a concomitant increase in proportion of homozygosity (and homozygous genotypes). Based on this trend, selections in the first few generations (F_2, F_3 or even F_4) will be concerned mainly with single-plant performance. Selections in later generations (F_5 and on) must shift towards line or family performance as the within-line variability becomes increasingly dissipated.

The pedigree selection method may be illustrated as in Figure 5 below.

Other notes of importance to pedigree selection are as follows:

(1) F_2 population provides the first opportunity to practise selection. Thus, progenies should be space-planted to facilitate the identification of superior types. Check varieties (one or the other parents or a successful cultivar) are planted every few rows, e.g. every 10th row, for comparison with the progenies. Oftentimes, undesirable progenies are eliminated as soon as they become visible. From the remaining plants, the best plants that exhibit the characteristics desired in a new variety are selected.

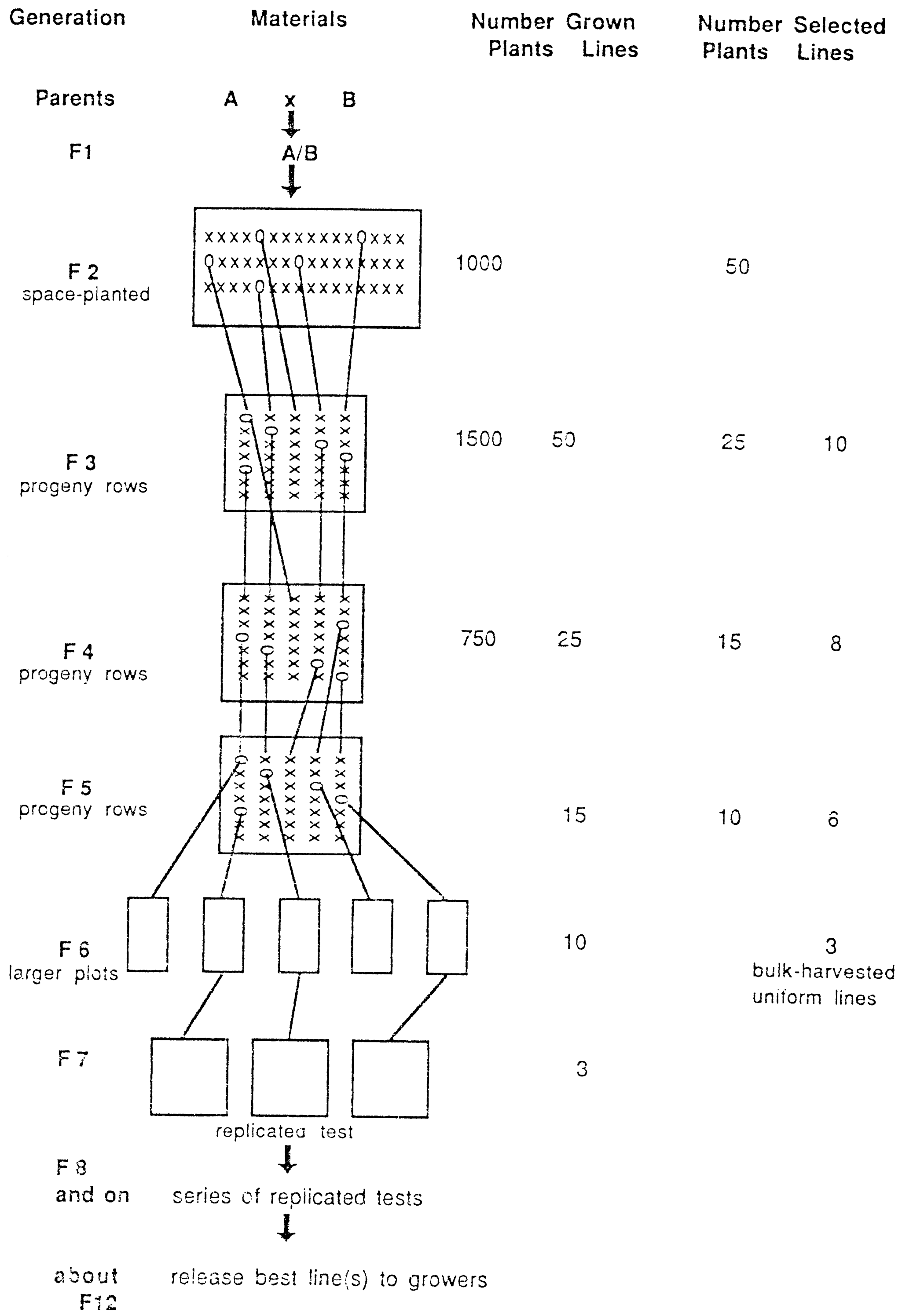

Figure 5. Diagrammatic sketch of pedigree selection method as applied to self-pollinated crops.

(2) F_3 families are also space-planted but normally at intervals closer than F_2 plants. Thirty-forty plants are usually grown to each F_3 family and check rows are again included. The potential of the cross will become apparent in the F_3. Single plant selection is again practised, selecting mainly from superior families but not neglecting superior progenies in otherwise poor families.

(3) Handling the F_4 generation is more or less similar to F_3. Sometimes, breeders prefer a shorter, multiple rows rather than a single long row for better visualization of the line potential. Many F_4 families will appear quite homogeneous but not in any magnitude that will suggest bulk-harvesting them. Still, single-plant selection are practicable, selecting only from mostly superior families. A combination of pedigree record and visual evaluation should lead to a substantial reduction in population size.

(4) Larger plots are used in the F_5 and spacing may approximate the commercial conditions. Single-plant selections are made usually from uniform families (they are therefore assumed to be largely homozygous). The bases of selection are pedigree record and visual appearance and possibly yield, if plots are large enough.

(5) The F_6 generation and beyond are considered non-segregating. Selection is shifted from single plant to family performance. Planting rates approximate as closely as possible the commercial conditions. Selected uniform families are harvested in bulk within each to provide sufficient seed stocks for the subsequent replicated trials.

Some modifications of the pedigree method that had been suggested involved: crossing superior selections in early generations or crossing of selections at random in the early generations. Both procedures are designed to slow down the approach to complete homozygosity and thus, enhance the chances of obtaining superior genetic combinations. The applicability of these modifications will depend on crop species–when crosses can be made easily, it should be appropriate to adopt them especially where linkage of traits under consideration are involved. They would be impractical, however, if crosses are difficult to make.

Pedigree method offers the following advantages: it permits elimination of a great number of unpromising materials in early generations; it allows evaluation of selections on the basis of several year's performance; and, it enables sampling more diverse materials from each cross.

However, the method is time-consuming, very tedious and therefore, severely limits the number of crosses that can be exploited as sources of superior genotypes.

Bulk method. Another simple and less time-consuming method of handling segregating progenies from hybridization involves growing them *en masse* from F_2 and succeeding generations until the desired homozygosity is achieved. The method allows natural selection, with the aid of the breeder, to gradually weed out the undesirable types within the population so that after a few generations only the most adapted forms are expected to remain. At this point, when such forms are already genetically stable (homozygous) , single plant selections are made and evaluated in a series of trials. Only the best line (s) are released.

Since very little work is required, bulk method allows several crosses to be handled at one time and large populations of each cross can be grown in each generation, thereby increasing the possibility of greater gene combinations. The bulk method is illustrated in

Figure 6 below. Sometimes, bulk method is modified in a manner that only the best plants in each generation (from F_2-F_5) are bulked. This is called modified bulk method.

Single-seed descent (SSD). As the name implies, breeding progenies in each generation are descended, technically speaking, each from a single seed. Usually, there is no selection from generation F_2 up to F_6 or F_7; as many plants as possible from the F_2 are carried down to F_6 or F_7 (at this time, the population will be made up largely of homozygous individuals). Evaluation of F_6 or F_7 lines and generations thereafter is carried out to select the superior combinations out of the cross.

SSD is very simple and could be a rapid method if manipulations of plant growth and development are done. Oftentimes, progenies are grown in the greenhouse to minimize losses in population size. This procedure will, however, require large greenhouse space and therefore, will allow handling of only a limited number of crosses. The underlying principle is to bring a wide range of the variability originally present in generation F_2 to a testable stage such as F_6 or F_7 where most lines would be genetically stable already.

A modification of SSD method often includes selection in the intervening generations especially for highly heritable traits (characters that are expressed strongly in single plants and not easily influenced by environment, e.g. disease resistances controlled by major genes). A good selection regime (or screening technique in the case of disease resistance) must be available however.

Assuming that two varieties are crossed to combine their desirable characteristics, a typical SSD method would be carried out as in Figure 7 below.

Backcross method. Literally speaking, backcross means "crossing back". The procedure is carried out using one of the original parents as a constant parent and the immediate or selected progenies from a segregating backcross generation as the other parent, depending upon the behaviour of the gene (s) under consideration. The constant parent is technically termed "recurrent parent". The other original parent which contributed the gene (s) under transfer to the recurrent parent is called "donor parent".

The objective of the backcross method is to transfer a gene or genes from the donor to the recurrent parent, recovering as much of the genetic background of the latter as desired. This implies that the recurrent parent must already be a successful variety, lacking only the gene (s) available from the donor to be truly outstanding. It also implies that the donor parent carries the gene (s) to be contributed in the most intense form.

The backcross method is especially applicable when the donor parent is a commercially unadapted type (e.g. wild species) so that straight hybridization and selection will not reasonably lead to superior genetic combinations. Often, the unadapted parent carries, along with the desired gene, a number of undesirable genes. Assuming no unfavorable linkage, backcross method will allow the transfer only of the desirable gene (s) , eliminating the undesirable traits in the backcrossing process. The method has been very useful in disease resistance breeding, where often only a few genes are being dealt with and therefore, the breeder is able to establish a firm control over the genetic circumstances.

For simplicity, assume that a single dominant gene for disease resistance is being transferred from a donor variety and that this gene is inherited in a dominant fashion. Using the letter "R" as gene symbol, *RR* and *Rr* would be resistant and *rr* is susceptible. In this situation, the donor parent is *RR* (resistant) and the recipient or recurrent parent is *rr* (susceptible). Under this given condition, the backcross method would be carried out as illustrated in Figure 8 below.

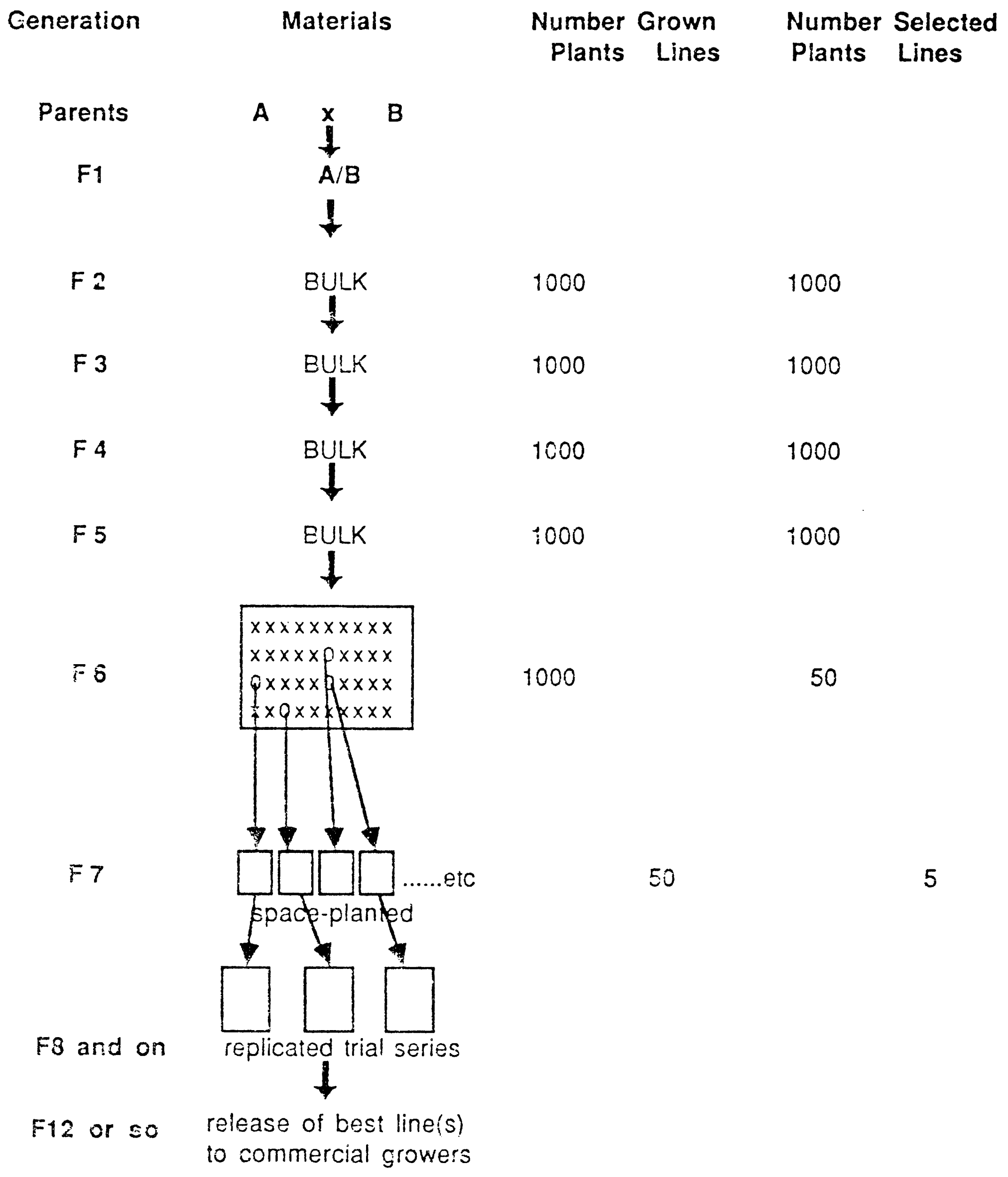

Figure 6. Diagrammatic sketch of the bulk method as applied to self-pollinated crops.

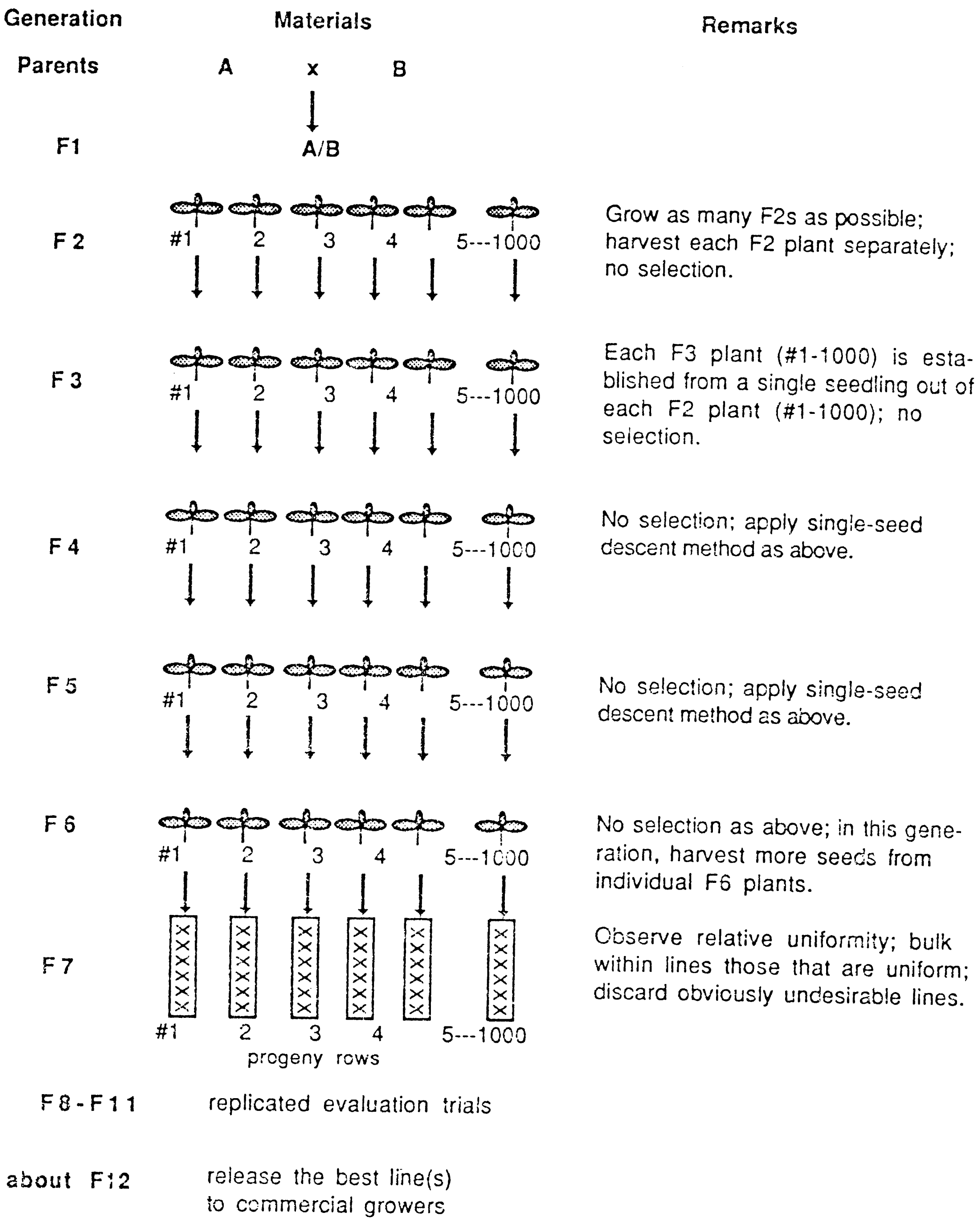

Figure 7. Diagrammatic sketch of the single-seed descent (SSD) method as applied to self-pollinated crops.

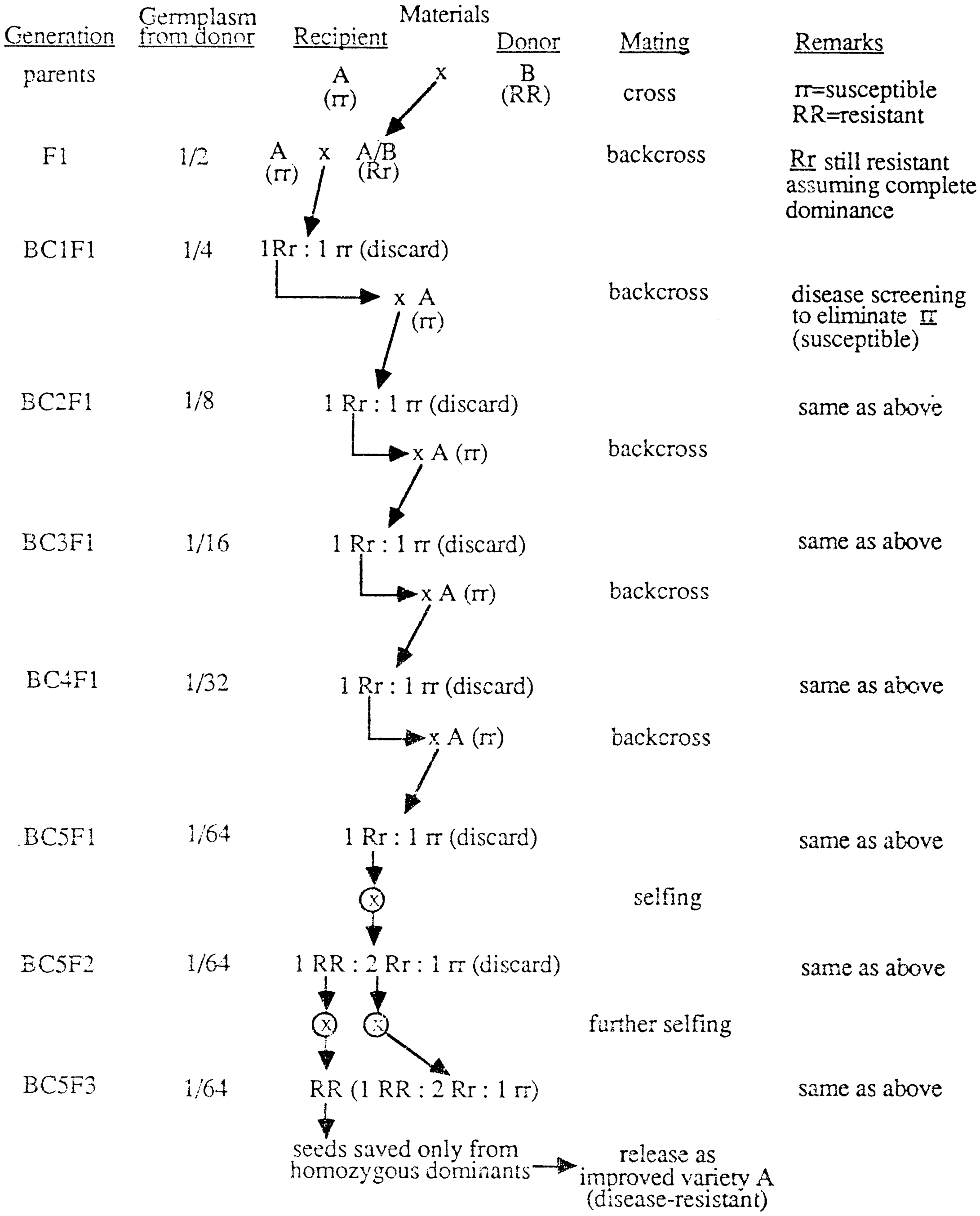

Figure 8. Diagrammatic sketch of the backcross method as applied to breeding for disease resistance, assuming single dominant gene control.

In every cross or backcross to the recurrent parent, the proportion of the genetic materials from the donor parent is reduced by one-half (1/2). In the F_1, this proportion is 1/2 or 50%. At the end of the 5th backcross, this proportion is only 1/64 or 1.6%. In other words, we would have recovered then approximately 98.4% of the genetic background of the recipient variety. If we designate the number of crosses and backcrosses to the recurrent parent as *b* , the proportion of germplasm from the donor parent is given by the formula:

$$\{ \text{Proportion of germplasm from donor parent} = (1/2)^b \}$$

Thus, after the initial cross (A/B) and 5 backcrosses, this proportion is $(1/2)^6$ or 1/64 or 1.6%.

The proportion of homozygosity and proportion of homozygous genotypes in any given backcross population are given by the same formula as that used in the selfing series, i.e.:

$$\{ \text{Proportion of homozygosity} = (2^m-1) / (2^m)\} ,$$
where m = number of backcross

and

$$\{ \text{Proportion of homozygous genotypes} = [(2^m-1) / (2^m)]^n \} ,$$
where m = number of backcrosses and
n = number of heterozygous loci in the
F_1 of the original cross

Using the above formula, the proportion of homozygous loci in the BC_5 population would be $(2^5-1) / (2^5) = 31/32$ or 96.9%, which is similar for the selfing series. Under backcrossing, however, the homozygous loci would be those of the recurrent parent and are not different combinations of loci from both parents as they would be under the selfing series. This is because much of the original genes from the donor has been dissipated through the backcross series.

Assuming that 10 loci are originally heterozygous in the F_1 and that 5 backcrosses were made, the proportion of homozygous genotypes in generation BC_5F_1 would be: $[(2^5 - 1) / 2^5]^{10} = (31 / 32)^{10}$ or 72.8%. In other words, 72.8% of the BC_5F_1 population would be like the recurrent parent.

Backcrossing a character determined by a single dominant gene is relatively easy. As the example above shows, successive backcrosses (assuming a good selection regime is available to identify the gene under transfer) can be carried out without an intervening selfing series. It is only at the end of the backcross program that the progeny tests are done to identify the homozygotes.

With a recessive gene under transfer, it is necessary to grow the backcross generation to F_2 to identify the homozygous recessive genotype prior to making the next backcross. Alternatively, two or three successive backcrosses may be done but the second or third backcross should be grown to F_2 to find the homozygous recessives prior to the next round of backcrosses.

The method is very effective with simply inherited characters (high heritability). However, its use is not precluded for complex quantitative traits. The backcross generations need to be grown to F_3 in this case to effectively identify the most intense expression of the

trait under transfer, i.e. evaluation is on family basis rather than single plant performance. If heritability of the traits is low, the F_2 and F_3 populations will have to be large.

Backcross method offers the following advantages : previous gains are not lost because improvements are made in a stepwise fashion; the program may be independent of the breeder's target environment; evaluations of the backcross varieties may not be necessary; it is relatively rapid; it is predictable; and it is repeatable.

The one disadvantage of the method is that, apart from the gain provided by the additional gene (s) incorporated, there is a ceiling to the performance of the backcross derivatives imposed by the potential of the recurrent variety. In other words, the method does not create unusual gene combinations which may by better than the recurrent parent. This is absolutely why the recurrent parent must already be a successful variety. Nonetheless, the method can be modified in such a manner that enough backcrosses may be made to recover in large part the genetic materials of the recurrent parent and yet, leave enough variability for exploitation by other breeding methods such as bulk, pedigree or its combination.

Development of hybrid cultivars. Nowadays, it is not uncommon to find F_1 hybrid varieties of self-pollinated crops released for commercial production. Hybrid varieties were originally popularized among cross-pollinated crops such as maize but the idea has caught on among a number of self-fertilized crops, e.g. tomato, even though the evidences on heterozygote advantage ("heterosis") have not been unequivocal.

It is true that F_1 hybrids do exhibit favorable traits such as uniformity and to some extent, better resistance to diseases, but their advantages over the standard cultivars have not been as great as in cross-pollinating species. The popularization of F_1 hybrids among self-fertilized species owes much to the "biological" rights they impart to their developer (oftentimes, private seed companies). By releasing F_1 hybrids, nobody outside the company can duplicate them since they are the sole possessor of the parental stocks. This set-up gives private seed industries a certain measure of business security.

The development of F_1 hybrids in self-pollinated crops follows to a large extent the scheme used for cross-pollinated species. Usually, established varieties are intercrossed in some systematic fashion to find those that nick well (good combining ability) with each other. Thereafter, these parental stocks are "built-up" often in stepwise fashion to cure the possible defects of their hybrids. Such defects may be disease susceptibility, poor quality, etc. (though the combination itself may be high-yielding). The use of backcross method in improving the parental stocks is common. Once the improved parental stocks are available, the original combinations that nicked well are repeated (but now using the improved parents) to form the F_1 hybrid varieties.

As self-pollinated crops often do not have the mechanisms of hybridity that cross-fertilized species possess, e.g. self-incompatibility, male sterility, dioecy, etc., hybrid seed production is manually done. This activity takes invariably many hours of skilled work (depending upon species), inputs that usually translate into added seed cost. Thus, hybrid seeds among self-pollinated crops are almost always very expensive.

Future Developments

Tomato breeders have accomplished a great deal in the past. Important horticultural traits such as enhanced yield, disease and pest resistance, better quality for fresh consumption and for processing, adaptability to environmental stresses, adaptability to machine-harvesting and

to processing, and a host of others, have been bred into modern-day commercial cultivars. Despite all these improvements, tomato breeders have barely exploited the vast reservoir of genetic variability within the genus *Lycopersicon*. The building blocks for further improvement of tomato are clearly available and expanded efforts to conserve, evaluate and utilize this variability are crucial (Tigchelaar 1986).

Conventional breeding techniques are still expected to be the mainstay of most future breeding efforts to exploit the variability in cultivated and wild relatives of tomato. Additional improvements in the traditional techniques may be expected to facilitate the breeding process but, it is safe to say, that the limits of conventional breeding methods have, for the most part, already been reached. New vistas in genetically improving tomatoes will have to be explored. It appears that the promise of the new field of biotechnology will find early applications in tomato breeding.

The exploitation of biotechnological tools to enhance the improvement of tomato is rapidly gaining momentum in the developed countries. While these novel technologies may need time to mature and be adopted in real-life agricultural situations, their impacts are potentially revolutionary. Some aspects of biotechnology such as direct engineering of disease and insect pest resistance genes are bound to augment the work of the plant breeders to produce characters that were not previously existing. A good example is the recent engineering of a new tomato which does not become soft because the genetic code controlling the softening enzyme has been inverted and thus, "deactivated".

Of immediate applicability as an "enhancer" tool of plant breeding is the RFLP (restricted fragment length polymorphism) method. RFLP will likely be integrated into existing plant breeding programs allowing researchers to access, transfer and combine genes at a rate and precision never before possible (Tanksley *et al.*, 1989; Young and Tanksley 1989). Using RFLP, complex characters may be reduced to simpler genetic components thereby enabling an increasingly well-controlled breeding of cultivars with combinations of traits previously too difficult or time-consuming to breed for. Furthermore, the transfer of important genes from the wild relatives of tomatoes will be expedited by RFLP–future cultivars are expected to have enhanced yield, resistance to insects and diseases, better adaptability and improved quality.

With respect to tomatoes in the developing world, AVRDC research has successfully brought the crop to adapt reasonably well to the hot and humid lowland tropics. Advanced tomato breeding lines are now available that resist the major diseases such as bacterial wilt, tomato mosaic virus and nematode, are tolerant to the hot wet tropical conditions, and bear fruits that are firm, of improved size and resistant to cracking. While relief through the revolutionary methods of biotechnology may take a while before it percolates to the developing countries, what advances in conventional breeding programs, such as that at AVRDC[9], are in store for tomatoes in the tropics?

With increasingly pressured environments, tropical tomatoes of the future will have to carry tolerances to more stresses than ever. On the biotic constraints, AVRDC's tropical tomato research seeks advances not only in the levels of disease resistance but also in the range of diseases that the advanced breeding lines would be resistant to. Progress in breeding for resistance to the following diseases are expected: viruses such as potato virus Y and

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9 AVRDC is also now gearing towards gaining the full benefits of developments in the field of biotechnology, if not fundamentally, at least in the aspects of adopting proven methods that will enhance the Center's role in vegetable improvement for the developing countries.

leafcurl; other bacterial diseases such as bacterial spot; and certain fungal diseases like black leafmold (*Cercospora fuligena*). Even resistances to unwieldy viruses, such as CMV, and equally important insects like fruitworm and aphids, may be unravelled as the potential of hitherto unexploited wild *Lycopersicon* and *Solanum* germplasm is widely explored. Multiple resistances to biotic stresses will have to be a standard feature of future tropical tomatoes.

The ability to set fruits under hot humid conditions is a basic feature of tropical tomatoes. This physiological asset needs to be reinforced in future breeding lines. Heat tolerance (specific for hot dry condition) , drought tolerance, tolerance of excess soil moisture, and even tolerance of poor soil fertility may all have to be added into the physiological arsenal of future tropical tomatoes.

Apart from more and better stress tolerances, tropical tomatoes of the future will need a significant upgrading of quality, especially in the readily apparent parameters of fruit acceptability like absence of cracks, reduced blotchy ripening, improved color, and increased longevity in transit or storage through better fruit firmness and/or prolonged ripening behavior.

As the food technology industry in the Asian region continue to grow, there will be an increasing demand for processed tomato products. A significant fraction of this need will still depend on importation; however, some countries especially those still strapped of foreign currency reserves, are expected to continue exploring the development of their native tomato processing industry. These countries will need better technology for processing tomato production, not only to enhance productivity but also to improve processing quality. The tropical processing tomatoes of the future will have to be better adapted to the tropics than they currently are; more and better levels of disease resistance and better processing quality will be needed. In special circumstances, adaptability to mechanical harvesting may be a necessary feature.

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